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The Global Carbon Cycle: A Test of Our Knowledge of Earth as a System

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Motivated by the rapid increase in atmospheric CO₂ due to human activities since the Industrial Revolution, several international scientific research programs have analyzed the role of individual components of the Earth system in the global carbon cycle. Our knowledge of the carbon cycle within the oceans, terrestrial ecosystems, and the atmosphere is sufficiently extensive to permit us to conclude that although natural processes can potentially slow the rate of increase in atmospheric CO₂, there is no natural "savior" waiting to assimilate all the anthropogenically produced CO₂ in the coming century. Our knowledge is insufficient to describe the interactions between the components of the Earth system and the relationship between the carbon cycle and other biogeochemical and climatological processes. Overcoming this limitation requires a systems approach.

Over the past 200 years, human activities have altered the global carbon cycle significantly. Understanding the consequences of these activities in the coming decades is critical for formulating economic, energy, technology, trade, and security policies that will affect civilization for

generations. Given present trends in energy demands, ample fossil fuel reserves, a lack of global, concerted, and alternative energy production strategies, and projections of human population growth, atmospheric CO₂ concentrations appear fated to increase throughout the coming century (1, 2). The rate of change in atmospheric CO₂ depends, however, not only on human activities but also on biogeochemical and climatological processes and their interactions with the carbon cycle. Here we examine some of the changes in biogeochemical and climatological processes concomitant with alterations in the carbon and nutrient cycles in the contemporary world, and compare these processes with our understanding of the preceding 420,000 years of Earth's history.

Entering Uncharted Waters

Under the auspices of the International Geosphere-Biosphere Programme (IGBP), several large international scientific studies have focused on elucidating various aspects of the global carbon cycle over the past decade (3). These programs have helped address two major recurrent questions in the current debate about global change: Can we distinguish between anthropogenic perturbations and natural variability in biogeochemical cycles and climate? And what is the sensitivity of Earth's climate to changes in atmospheric CO₂? We consider the two questions in the context of the relatively recent geological history of Earth, for which we have robust paleoclimatological proxies.

Arrhenius recognized over 100 years ago (4) that atmospheric CO₂ plays a critical role in regulating Earth's temperature (5, 6). Analyses of ice cores strongly suggest that

over the past 420,000 years, the climate system has operated within a relatively constrained domain of atmospheric CO₂ and temperature (7, 8) (Fig. 1). In the CO₂-temperature phase space that characterized the preindustrial world, CO₂ oscillated in 100,000-year cycles by approximately 100 parts per million by volume (ppmv), between about 180 and 280 ppmv. On millennial time scales, changes in CO₂ recorded in ice cores are highly correlated with changes in temperature (9). Although high-resolution analysis of ice cores suggests that there are periods in Earth's history when temperature can change relatively sharply without a discernible change in CO₂ (7), the converse does not appear to be true.

Comparison of the present atmospheric concentration of CO₂ with the ice core record reveals that we have left the domain that defined the Earth system for the 420,000 years before the Industrial Revolution (10) (Fig. 1). Atmospheric CO₂ concentration is now nearly 100 ppmv higher, and has risen to that level at a rate at least 10 and possibly 100 times faster than at any other time in the past 420,000 years. We have driven the Earth system from the tightly bounded domain of glacial-interglacial dynamics. Are we in a transition period to a new, stable domain? If so, what are the main forcing factors and feedbacks of this transition? What will be the climatological features of a new domain? What will be the responses and feedbacks of Earth's ecosystems? How and when can and should we return to the preindustrial domain?

The active carbon reservoirs and their strengths. Atmospheric CO₂ exchanges rapidly with oceans and terrestrial ecosystems (11). The ratio between the rate at which these two reservoirs absorb atmospheric CO₂ and the rate of emissions determines the overall rate of change of atmospheric CO₂. The sink strength of the reservoirs determines the capacity to absorb excess or anthropogenic CO₂. During glacial-interglacial transitions, for example, the atmosphere acts to transfer carbon between terrestrial ecosystems and the oceans. The remarkable consistency of the upper and lower limits of the glacial-interglacial atmospheric CO₂ concentrations, and the apparent fine control over periods of many thousands of years around those limits, suggest strong feedbacks that constrain the sink

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strengths in both the oceans and terrestrial ecosystems. The relatively rapid transition from glacial to interglacial states and the initially steep, but eventually gradual, transition into glacial periods (8) suggests that the rates of absorption and emission of CO_2 from the oceans and terrestrial ecosystems are asymmetrical. It should be noted that because of this asymmetry, the average atmospheric CO_2 concentration during the past 420,000 years was only ~ 220 ppmv, not 280 ppmv as usually ascribed (12).

How is atmospheric CO_2 regulated? The total of dissolved inorganic carbon in the oceans is 50 times that of the atmosphere (Table 1), and on time scales of millennia, the oceans determine atmospheric CO_2 concentrations, not vice versa. Atmospheric CO_2 continuously exchanges with oceanic CO_2 at the surface. This exchange, which amounts to ~ 90 gigatons (Gt) of carbon per year in each direction, leads to rapid equilibration of the atmosphere with the surface water. Upon dissolution in water, CO_2 forms a weak acid that reacts with carbonate anions and water to form bicarbonate. The capacity of the oceanic carbonate system to buffer changes in CO_2 concentration is finite and depends on the addition of cations from the relatively slow weathering of rocks. Because the rate of anthropogenic CO_2 emissions is several orders of magnitude greater than the supply of mineral cations, on time scales of millennia the ability of the surface oceans to absorb CO_2 will inevitably decrease as the atmospheric concentration of the gas increases (13).

The concentration of total dissolved inor-

ganic carbon in the ocean increases markedly below about the upper 300 m, where it remains significantly above the surface ocean-atmosphere equilibrium value in all ocean basins. The higher concentration of inorganic carbon in the ocean interior results from a combination of two fundamental processes: the "solubility pump" and "biological pumps" (14, 15).

The efficiency of the solubility pump depends on the thermohaline circulation and on latitudinal and seasonal changes in ocean ventilation (16, 17). CO_2 is more soluble in cold, saline waters, and sequestration of atmospheric CO_2 in the ocean interior is therefore controlled by the formation of cold, dense water masses at high latitudes, especially in the North Atlantic and in the Southern Ocean confluence. As these water masses sink into the ocean interior and are transported laterally, CO_2 is effectively prevented from re-equilibrating with the atmosphere by a cap of lighter overlying waters. Re-equilibration occurs only when waters from the ocean interior are brought back to the surface, decades to several hundreds of years later.

Coupled climate-ocean simulations (6, 18) suggest that CO_2 -induced global warming will lead to increased stratification of the water column. If this occurs, the transport of carbon from the upper ocean to the deep ocean will be reduced, with a resulting decrease in the rate of sequestration of anthropogenic carbon in the ocean (19, 20). The combined effects of progressive saturation of the buffering capacity and increased stratification will weaken two important negative feedbacks in the carbon-climate system,

thereby reducing the rate of oceanic uptake of anthropogenic CO_2 . The magnitude of these feedbacks is critically dependent on how ocean circulation and mixing will respond to the climatic forcing.

Biological processes also contribute to the absorption of atmospheric CO_2 in the ocean. Phytoplankton photosynthesis lowers the partial pressure of CO_2 in the upper ocean and thereby promotes the absorption of CO_2 from the atmosphere. Approximately 25% of the carbon fixed in the upper ocean sinks into the interior (21, 22), where it is oxidized through heterotrophic respiration, raising the concentration of dissolved inorganic carbon (DIC). The export of organic carbon from the surface to the ocean interior presently accounts for ~ 11 to 16 Gt of carbon per year (23). This process keeps atmospheric CO_2 concentrations 150 to 200 ppmv lower than they would be if all the phytoplankton in the ocean were to die (23, 24). In addition to the organic biological pump, several phytoplankton and zooplankton species form CaCO_3 shells that sink into the interior of the ocean, where some fraction dissolves. This inorganic carbon cycle leads to a reduction in surface ocean DIC relative to the deep ocean and is therefore sometimes called the "carbonate pump." The process of precipitating carbonates, however, increases the partial pressure of CO_2 (25). Hence, on time scales of centuries, while the carbonate pump lowers DIC concentrations in the upper ocean, it simultaneously leads to the evasion of CO_2 from the ocean to the atmosphere.

Coupled climate-biogeochemical models suggest that the biological pumps tend to counteract the decrease in uptake caused by the solubility pump (20, 26). If the biological pumps are to absorb anthropogenic CO_2 in the coming century, their efficiency must increase. In principle, this can be accomplished by any or all of four processes: (i) enhancing utilization of excess nutrients in the upper ocean, (ii) adding one or more nutrients that limit primary production, (iii) changing the elemental ratios of the organic matter in the ocean, and (iv) increasing the organic carbon/calcite ratio in the sinking flux (27). There are significant gaps in our knowledge that limit our ability to predict the magnitude of changes in oceanic uptake, but the likely changes in the biological pump are too small to counteract the projected CO_2 emissions in the coming century. Almost certainly, however, changes in oceanic ecosystem structure will accompany changes in physical circulation (and hence changes in nutrient supplies), lowered pH, and changes in the hydrological cycle. Our present knowledge of the factors that determine the abundance and distribution of key groups of marine organisms is so limited that it is unlikely we will be able to predict such changes within the next decade

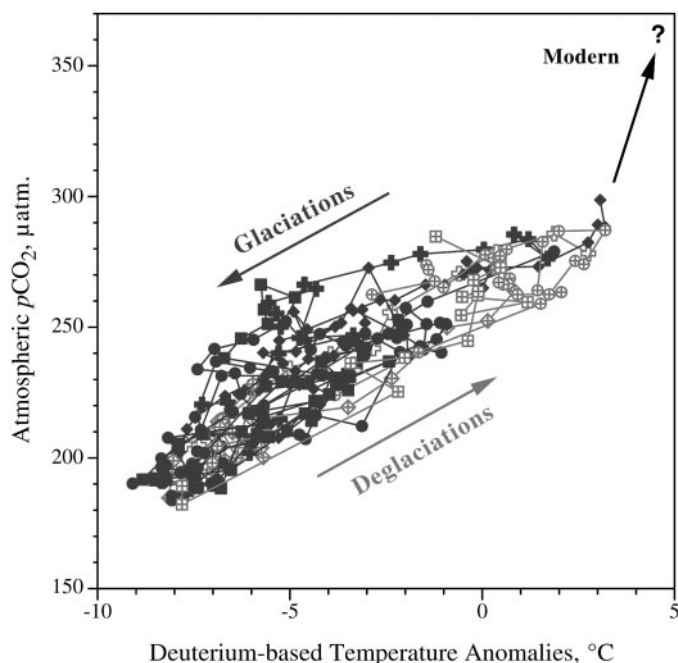


Fig. 1. A correlation between atmospheric partial pressure of CO_2 ($p\text{CO}_2$) and isotopic (δ_D) temperature anomalies as recorded in the Vostok ice core. The figure shows that climate variations in the past 420,000 years operated within a relatively constrained domain. Data are from (8).

with reasonable certainty (28). These uncertainties affect our ability to predict specific responses, but not the sign of the changes in atmospheric CO₂ or the impact of this change on upper ocean pH. If our current understanding of the ocean carbon cycle is borne out, the sink strength of the oceans will weaken, leaving a larger fraction of anthropogenically produced CO₂ in the atmosphere or to be absorbed by terrestrial ecosystems.

Terrestrial ecosystems also exchange CO₂ rapidly with the atmosphere, but unlike in the oceans, there is no physicochemical pump. CO₂ is removed from the atmosphere through photosynthesis and stored in organic matter. It is returned to the atmosphere via a number of respiratory pathways that operate on various time scales: (i) autotrophic respiration by the plants themselves; (ii) heterotrophic respiration, in which plant-derived organic matter is oxidized primarily by soil microbes; and (iii) disturbances, such as fire, in which large amounts of organic matter are oxidized in very short periods of time.

On a global basis, terrestrial carbon storage primarily occurs in forests (29). The sum of carbon in living terrestrial biomass and soils is approximately three times greater than the CO₂ in the atmosphere (Table 1), but the turnover time of terrestrial carbon is on the order of decades. Direct determination of changes in terrestrial carbon storage has proven extremely difficult (30). Rather, the contribution of terrestrial ecosystems to carbon storage is inferred from changes in the concentrations of atmospheric gases, especially CO₂ and O₂, their isotopic composition, inventories of land use change, and models (31–33). The models require accurate knowledge of the oceanic uptake of CO₂ (31, 34, 35).

Terrestrial net primary production (NPP) (36) is not saturated by present atmospheric CO₂ concentrations (37). Consequently, as atmospheric CO₂ increases, terrestrial plants are a potential sink for anthropogenic carbon. The principal carbon-fixing enzyme in plants is ribulose 1,5-bisphosphate carboxylase/oxygenase (rubisco) (38). In C3 plants, the activity of rubisco increases with increasing CO₂ concentrations, saturating between 800 and 1000 ppmv CO₂, a concentration that will probably be reached early in the next century at the present emissions rate (2). Because the saturation function decreases as CO₂ increases, terrestrial plants will become less of a sink for CO₂ in coming decades. Some experimental evidence suggests that because of nutrient limitation (39), NPP may level off at only 10 to 20% above current rates, at an atmospheric CO₂ concentration of 550 to 650 ppmv, or double preindustrial concentrations (40). Furthermore, increased temperature will probably lead to higher microbial heterotrophic respiration, which may

counteract and even exceed the enhancement of NPP (41). The combined effects of higher CO₂ concentrations, higher temperatures, and changes in disturbance and soil moisture regimes lead to considerable uncertainty about the ability of terrestrial ecosystems to mitigate against rising CO₂ in the coming decades (42). However, recent results from long-term soil warming experiments in a boreal forest contradict the idea that the projected rise in temperature is likely to lead to forests that are now carbon sinks becoming carbon sources in the foreseeable future (43).

Again, as in the case of marine ecosystems, we can predict that the negative feedback afforded by terrestrial ecosystems in removing anthropogenic CO₂ from atmosphere will continue; however, the sink strength will almost certainly weaken. The exact magnitude of the change in sink strength remains unclear.

Interaction of the carbon cycle with other biogeochemical cycles. All biotic sinks for CO₂ require other nutrients in addition to carbon. Humans have affected virtually every major biogeochemical cycle (Table 2), but the effects of these impacts on the interactions between these elemental cycles are poorly understood (44). The production of synthetic fertilizers, the cultivation of nitrogen-fixing crops, and the deposition of fossil fuel-associated nitrogen are collectively of the same order of magnitude as natural biological nitrogen fixation (45). These inputs will continue to rise with the projected increase in human population (46). Similarly, there has been an approximately fourfold increase in phosphorus inputs to the biosphere, primarily due to mining of phosphorus compounds for fertilizer.

At first glance, one might conclude that simultaneous increases in nitrogen fixation and phosphate production would stimulate the biological sequestration of carbon in terrestrial and marine ecosystems. Will such stimulation provide salvation from the continued anthropogenic emissions of CO₂ to the atmosphere?

It is estimated that by 2050, the total transport of fixed inorganic nitrogen from land to the coastal zone will have increased from the present value of ~20 teragrams (Tg) of nitrogen to ~40 Tg of nitrogen per year (47), concomitant with an increase in human population from 6 to 9 or 10 billion. Although nutrient loading has resulted in coastal eutrophication on a global scale (48), denitrification presently removes virtually all land-derived nitrogen before it can reach the open ocean (49, 50). Coastal denitrification thus effectively decouples the terrestrial and oceanic nitrogen cycles. However, even if no denitrification occurred, the increased flux of land-derived nitrogen would sequester only 0.4 Gt of carbon per year (48), corresponding

to about 5% of the present anthropogenic CO₂ emissions.

There is no evidence that phosphorus significantly limits primary production in coastal or open oceans on a global scale (51) or that phosphorus loading of the coastal oceans has significantly altered global primary production (46).

Iron is a micronutrient that limits both primary production (52) and nitrogen fixation in many areas of the ocean (53). Eolian (windborne) iron fluxes, a principal source of iron input to the open ocean, are coupled both to land use and the hydrological cycle (54). Episodic aridity affects eolian iron supplies, and in the coming decades, iron fluxes to the ocean could therefore increase because of increased evaporation of soil moisture or decrease because of increased precipitation (55). Increases in evaporation and increases in precipitation are expected in different parts of the land surface in response to increasing global temperatures. Thus, although increasing temperature and its potential influence on the availability of iron in the open ocean will affect the biological uptake of carbon in the ocean, at present we do not know the sign of the changes. However, even if iron fluxes were to increase to such an extent that oceanic nitrogen fixation were stimulated to the maximum, the maximum change in atmospheric CO₂ that could ensue would be about 40 ppmv. Although not insignificant, such an effect is unrealistic on time scales of centuries (56).

Eolian nitrogen inputs can also potentially enhance both terrestrial and marine uptake of anthropogenic CO₂ (37). In terrestrial ecosystems, the sink strength resulting from eolian nitrogen deposition depends on the carbon: nitrogen ratio of the stored organic mat-

Table 1. Carbon pools in the major reservoirs on Earth.

Pools	Quantity (Gt)
Atmosphere	720
Oceans	38,400
Total inorganic	37,400
Surface layer	670
Deep layer	36,730
Total organic	1,000
Lithosphere	
Sedimentary carbonates	>60,000,000
Kerogens	15,000,000
Terrestrial biosphere (total)	2,000
Living biomass	600–1,000
Dead biomass	1,200
Aquatic biosphere	1–2
Fossil fuels	4,130
Coal	3,510
Oil	230
Gas	140
Other (peat)	250

ter and the degree of nitrogen saturation of soils (44, 57–59). Nitrogen deposition is predicted to continue and has the potential to enhance the carbon sink in nitrogen-limited ecosystems, but it will probably become decreasingly effective at doing so. Future nitrogen deposition will largely occur on already nitrogen-saturated soils, such as in the forests of Western Europe, China, and India, and on agricultural lands in the tropics, whose capacity to sequester carbon is intrinsically small

and where soils are mostly limited by phosphate (57). In the context of the global carbon cycle, the eolian input of nitrogen to marine ecosystems is essentially irrelevant (59).

In addition to ecophysiological considerations, land use change plays a major role in the carbon source/sink dynamics. The increased pressure in the developing world to increase food and fiber production by converting forests to agricultural use effectively increases the flux of carbon to the atmosphere

while simultaneously reducing the land area available for active sinks. Abandonment of agricultural land and regrowth of forests, largely in the temperate Northern Hemisphere, may be a significant terrestrial CO₂ sink at present (34) but cannot be sustained indefinitely. This sink can buy some time, but unless CO₂ emissions are reduced, it cannot mitigate against continued accumulation of the gas in Earth's atmosphere given projected emission scenarios.

Table 2. Examples of human intervention in the global biogeochemical cycles of carbon, nitrogen, phosphorus, sulfur, water, and sediments. Data are for the mid-1900s.

Element	Flux	Magnitude of flux (millions of metric tons per year)		% change due to human activities
		Natural	Anthropogenic	
C	Terrestrial respiration and decay CO ₂	61,000		
	Fossil fuel and land use CO ₂		8,000	+ 13
N	Natural biological fixation	130		
	Fixation owing to rice cultivation, combustion of fossil fuels, and production of fertilizer		140	+ 108
P	Chemical weathering	3		
	Mining		12	+ 400
S	Natural emissions to atmosphere at Earth's surface	80		
	Fossil fuel and biomass burning emissions		90	+ 113
O and H (as H ₂ O)	Precipitation over land	111 × 10 ¹²		
	Global water usage		18 × 10 ¹²	+ 16
Sediments	Long-term preindustrial river suspended load	1 × 10 ¹⁰		
	Modern river suspended load		2 × 10 ¹⁰	+ 200

The Need for an Integrated Systems Approach

The global carbon cycle is affected by human activities and is coupled to other climatological and biogeochemical processes. As discussed above, we have considerable information about specific aspects of the carbon cycle, but many of the couplings and feedbacks are poorly understood. As we drift further away from the domain that characterized the preindustrial Earth system, we severely test the limits of our understanding of how the Earth system will respond.

A look at the current understanding of glacial-interglacial CO₂ changes illustrates the problem. Perhaps surprisingly, there is no consensus on the causes of these changes. There are at least 11 hypotheses (53, 60, 61), which may be grouped into three basic themes: (i) physical/chemical “reorganization” of the oceans, (ii) changes in the ocean carbonate system, and (iii) changes in ocean nutrient inventories. Many of these hypotheses are not mutually exclusive. The interactions between marine and terrestrial ecosystems, changes in ocean circulation, radiative forcing, and greenhouse gases all probably interact in a specific sequence to give rise to the natural cyclic atmospheric and climatic oscillations. These interactions are not presently represented in detailed models of the glacial-interglacial transitions.

This example illustrates three points. First, in the recent history of Earth, the carbon cycle did not operate in a vacuum and was not constrained to a specific reservoir. Natural changes in the inventories of carbon, as inferred from the ice core records of glacial-interglacial transitions, are linked to other biogeochemical and climatological processes. Those linkages continue to the present, but the quantitative impacts in the coming century are obscured by simultaneous alterations of numerous biogeochemical cycles through human activities. Second, the scientific community has generally approached problems such as glacial-interglacial transitions from a disciplinary perspective. This approach has not produced completely satisfactory explanations for what is clearly a large natural perturbation in the global carbon cycle. Because of the disciplinary nature of research, interactions between

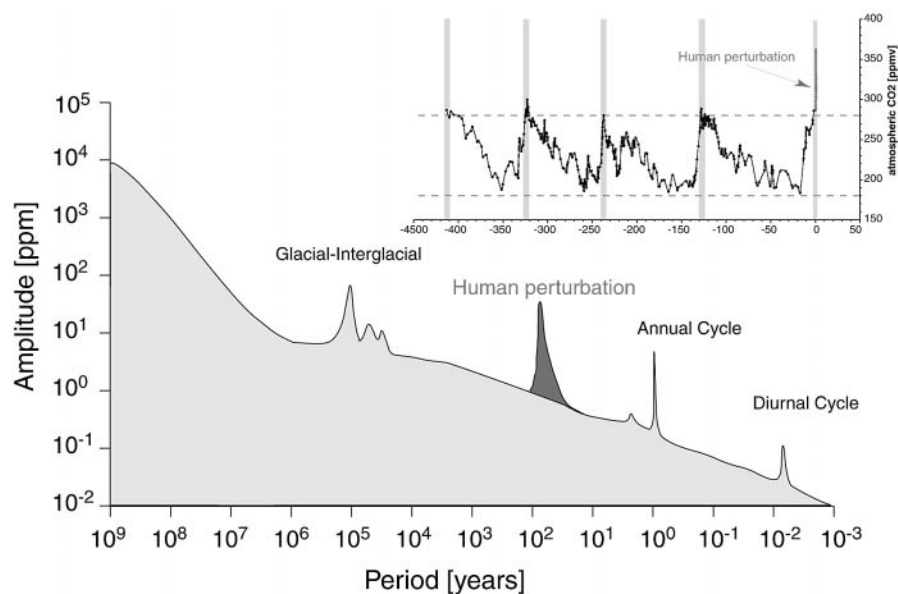


Fig. 2. Schematic variance spectrum for CO₂ over the course of Earth's history. Note the impact of human perturbations on the decade-to-century scale. (Inset) Changes in atmospheric CO₂ over the past 420,000 years as recorded in the Vostok ice, showing that both the rapid rate of change and the increase in CO₂ concentration since the Industrial Revolution are unprecedented in recent geological history.

components of the Earth system are not incorporated into present biogeochemical or climate models. When changes in isolated processes are considered, we usually understand the signs of feedbacks, if not the magnitudes of the responses. It is when processes interact that we have significant problems in reproducing the phenomena quantitatively. Clearly, a systems approach is needed. Third, reconstructions of the carbon cycle (for example, during glacial-interglacial transitions) provide testable hypotheses about the Earth system. Consensus on how a 100-ppmv change in atmospheric CO₂ can occur naturally within a 100,000-year time frame (62) would imply some understanding of the feedbacks within the Earth system. Knowledge of these feedbacks does not give us predictive capability for the coming decades or centuries, but it can help us develop the modeling tools needed to integrate the detailed information gathered from component studies of the contemporary world.

Our analysis above shows that although natural sinks can potentially slow the rate of increase in atmospheric CO₂, there is no natural savior waiting to assimilate all the anthropogenic CO₂ in the coming century. Although on geological time scales the anthropogenic emission of CO₂ is a transient phenomenon (Fig. 2), it will affect Earth's biogeochemical cycles for hundreds of years to come (20, 63). Our present imperfect models suggest that the feedbacks between carbon and other biogeochemical and climatological processes will lead to weakened sink strengths in the foreseeable future, and the prospects of retrieving anthropogenic CO₂ from the atmosphere by enhancing natural sinks are small. This condition cannot persist indefinitely. Potential remediation strategies, such as the purposeful manipulation of biological and chemical processes to accelerate the sequestration of atmospheric CO₂, are being seriously considered by both governmental bodies and private enterprises. These mitigation strategies will themselves have unknown consequences and must be carefully assessed within the context of an integrated systems approach before any action is taken.

As we rapidly enter a new Earth system domain, the "Anthropocene" Era (64), the debate about distinguishing human effects from natural variability will inevitably abate in the face of increased understanding of climate and biogeochemical cycles. Our present state of uncertainty arises largely from lack of integration of information. Nevertheless, scientists' abilities to predict the future will always have a component of uncertainty. This uncertainty should not be confused with lack of knowledge nor should it be used as an excuse to postpone prudent policy decisions based on the best information available at the time.

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- The reconstruction of paleotemperatures from the ice cores is based on the H/D and ¹⁸O/¹⁶O fractionation in the precipitation. Necessarily, the inferred temperature is that of the upper troposphere, not that at ground level. Moreover, the inferred temperature is not a global mean but rather a value for the region, in this case, Vostok in Antarctica. Despite these caveats, the glacial-interglacial temperature trends and anomalies are highly consistent on time scales of 100,000 years for the four cycles obtained from the ice core.
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- On time scales of millions of years, vulcanism and weathering reactions are critical determinants of atmospheric CO₂. The weathering reactions can be summarized by the following:

$$\text{CO}_2 + \text{CaSiO}_3 \rightleftharpoons \text{CaCO}_3 + \text{SiO}_2$$
 where Mg can substitute for Ca. CO₂ is resupplied to the atmosphere by vulcanism [J. F. Kasting, O. B. Toon, J. B. Pollack, *Sci. Am.* **258**, 90 (1988)]. On time scales of decades, these processes are relatively insignificant in determining atmospheric CO₂ as compared with the exchanges of CO₂ between oceanic and terrestrial ecosystems.
- The preindustrial concentration of CO₂ was ~280 ppmv throughout the Holocene. The lower mean value is due to the fact that the glacial periods (with low CO₂ concentrations) were about four times longer than the interglacial periods. In fact, most of the recent history of Earth is dominated by a glacial climate, with relatively short punctuations of interglacial phases. If the low CO₂ levels of glacial periods had persisted through the Holocene, plants that provided food and fiber for early human civilization may not have been cultivatable [R. F. Sage, *Global Change Biology* **1**, 93 (1995)].
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- This is the apparent steady-state value, not the change in the net exchange with the atmosphere.
- This so-called "Strangelove" ocean scenario is uncertain within about a factor of 2 because we do not have better estimates of export fluxes of carbon in the oceans (22).
- This (perhaps counterintuitive) effect is a direct outcome of the calcification reaction, which can be summarized as 2HCO₃ + Ca ↔ CaCO₃ + CO₂ + H₂O. The mean residence time of Ca in the oceans is 8.5 × 10⁵ years (it is even longer for Mg²⁺). On time scales of millions of years, as the Ca supply from weathering keeps pace with the precipitation of carbonates, carbonate formation and burial become significant sinks for CO₂. In fact, carbonates are the largest reservoir of carbon on Earth (Table 1). As CO₂ dissolves in seawater, it forms carbonic acid, which lowers pH (13). Thus, as atmospheric CO₂ increases, the pH of the upper ocean decreases until the buffering capacity of the ocean is restored by the dissolution of carbonates.
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- The storage of carbon in terrestrial ecosystems is primarily related to the relative resistance of lignin and other polymeric carbon complexes to degradation or herbivory. Terrestrial plants contain, on average, substantially more organic carbon per unit of nitrogen or phosphorus than their marine counterparts, the phytoplankton, which are primarily composed of protein. Although lignins and other carbon-rich polymers may accumulate in terrestrial ecosystems on time scales of decades, on longer time scales most of these molecules are oxidized, so that the accumulation of organic carbon in soils is a minuscule fraction of the total carbon fixed by the ecosystem. Lakes may also store substantial amounts of organic matter in sediments [W. E. Dean and E. Gorham, *Geology* **26**, 535 (1998)].
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